3-2017

Long-term spatial heterogeneity in mallard distribution in the Prairie pothole region

Adam K. Janke
Iowa State University, ajanke@iastate.edu

Michael J. Anteau
United States Geological Survey

Joshua D. Stafford
United States Geological Survey

Wildlife Society Bulletin 41(1):116–124; 2017; DOI: 10.1002/wsb.747

Original Article

Long-Term Spatial Heterogeneity in Mallard Distribution in the Prairie Pothole Region

ADAM K. JANKE,[1] *Department of Natural Resource Ecology and Management, Iowa State University, 339 Science Hall II, Ames, IA 50011, USA*
MICHAEL J. ANTEAU, *U.S. Geological Survey, Northern Prairie Wildlife Research Center, 8711 37th Street Southeast, Jamestown, ND 58401, USA*
JOSHUA D. STAFFORD, *U.S. Geological Survey, South Dakota Cooperative Fish and Wildlife Research Unit, Department of Natural Resource Management, South Dakota State University, Box 2140 B, Biostress Lab, Brookings, SD 57007, USA*

ABSTRACT The Prairie Pothole Region (PPR) of north-central United States and south-central Canada supports greater than half of all breeding mallards (*Anas platyrhynchos*) annually counted in North America and is the focus of widespread conservation and research efforts. Allocation of conservation resources for this socioeconomically important population would benefit from an understanding of the nature of spatiotemporal variation in distribution of breeding mallards throughout the 850,000 km^2 landscape. We used mallard counts from the Waterfowl Breeding Population and Habitat Survey to test for spatial heterogeneity and identify high- and low-abundance regions of breeding mallards over a 50-year time series. We found strong annual spatial heterogeneity in all years: 90% of mallards counted annually were on an average of only 15% of surveyed segments. Using a local indicator of spatial autocorrelation, we found a relatively static distribution of low-count clusters in northern Montana, USA, and southern Alberta, Canada, and a dynamic distribution of high-count clusters throughout the study period. Distribution of high-count clusters shifted southeast from northwestern portions of the PPR in Alberta and western Saskatchewan, Canada, to North and South Dakota, USA, during the latter half of the study period. This spatial redistribution of core mallard breeding populations was likely driven by interactions between environmental variation that created favorable hydrological conditions for wetlands in the eastern PPR and dynamic land-use patterns related to upland cropping practices and government land-retirement programs. Our results highlight an opportunity for prioritizing relatively small regions within the PPR for allocation of wetland and grassland conservation for mallard populations. However, the extensive spatial heterogeneity in core distributions over our study period suggests such spatial prioritization will have to overcome challenges presented by dynamic land-use and climate patterns in the region, and thus merits additional monitoring and empirical research to anticipate future population distribution. Published 2017. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS *Anas platyrhynchos*, breeding distribution, hot-spot analysis, Prairie Pothole Region, spatial heterogeneity.

Appropriate allocation of resources is essential for successful conservation outcomes among declining or socioeconomically important wildlife populations. Primary considerations for effective allocation of conservation are 1) what point in a species' life cycle is most limiting population growth; and 2) where within the species' distribution is it most efficient to focus conservation efforts? Identification of important life-cycle periods for conservation has received considerable study in many populations and is informed by predictive population modeling based on demographic parameters measured within the population or among individuals (Bradbury et al. 2001). Objective spatial prioritization of conservation based on long-term monitoring of species distributions is an emerging discipline and has the unique challenge of integrating population ecology with spatially heterogeneous constraints of land use and valuation (Whittaker et al. 2005, Wilson et al. 2006, Franklin 2010). Together, targeting important landscapes during life-cycle phases most limiting to population growth can yield the best prospects for achieving desired conservation outcomes.

The North American mallard (*Anas platyrhynchos*) population has been the focus of wide-spread conservation and research because of their socioeconomic importance as a game species and potential to serve as an umbrella species for conservation of wetland habitats throughout their range. Extensive research throughout the life cycle of North American mallards has shown population growth is sensitive to variation in vital rates during the breeding season (Hoekman et al. 2002, Howerter et al. 2014). Therefore, mallard breeding habitats and behavior has become a conservation and research priority. Research on the breeding grounds has described intrinsic and extrinsic factors influencing reproductive success

Received: 17 May 2016; Accepted: 25 November 2016
Published: 21 March 2017

[1]*E-mail: ajanke@iastate.edu*

of mallards (e.g., Krapu et al. 1997, Devries et al. 2008, Howerter et al. 2014) and factors influencing their continental distribution (e.g., Johnson and Grier 1988, Cowardin et al. 1995). Collectively, this research has definitively established the importance of the Prairie Pothole Region (PPR) as the core breeding range.

The PPR is approximately 850,000 km^2 and annually hosts an estimated 5.1 million breeding mallards, accounting for an average 65.4% of the breeding population traditionally estimated by the U.S. Fish and Wildlife Service (USFWS) and Canadian Wildlife Service (CWS; Batt et al. 1989; Table S1, available online in Supporting Information). The midcontinent population of mallards breeding in the PPR accounts for a large portion of the annual mallard harvest in the Mississippi and Central Flyways and therefore, has positive effects on local economies and conservation throughout the United States (Munro and Kimball 1982, Vrtiska et al. 2013). The PPR was identified as "a top priority" for North American waterfowl conservation in the North American Waterfowl Management Plan (NAWMP) because of its importance to waterfowl (NAWMP Committee 2012:32). Although the PPR as a whole is an important driver of mallard population dynamics, spatial variability in climate and land use in the region creates considerable heterogeneity in mallard habitat availability throughout the region (Bethke and Nudds 1995, Miller 2000, Doherty et al. 2015). Understanding the distributional patterns that result from this habitat heterogeneity could improve conservation delivery for mallards and other sympatric wetland- and grassland-dependent wildlife in the region (Doherty et al. 2015).

There is wide-spread interest in waterfowl population dynamics in North America (e.g., Johnson et al. 2002, Johnson 2011); therefore, USFWS and CWS annually conduct the Waterfowl Breeding Population and Habitat Survey (WBPHS), which is an intensive and geographically broad monitoring program to count breeding waterfowl in their core northern breeding ranges dating back to the 1950s (Smith 1995). The geographic extent and temporal continuity of the survey, particularly within the PPR, is unprecedented among many wildlife species and affords a unique opportunity to evaluate the spatial distribution of breeding mallards over half a century in their core breeding range. We used these data to characterize heterogeneity in mallard abundance through time within the PPR and generate hypotheses about factors influencing their distribution. Applying our results can aid in prioritizing landscapes for conservation in the region and making predictions about how mallards may respond to changes in breeding habitats in future land use and climate scenarios.

STUDY AREA

We conducted our research in the PPR of north-central United States and southern Prairie Canada. The approximately 850,000-km^2 area comprises portions of 3 provinces and 5 U.S. States, though our analyses were constrained to the Alberta, Saskatchewan, Manitoba, Canada, and North Dakota, South Dakota, and Montana, USA, where survey data for mallards were available. The region was characterized by millions of depressional wetlands with varying hydroperiods and annual recurrence patterns as described in a number of previous studies (e.g., Johnson and Grier 1988, Johnson and Higgins 1997, Niemuth et al. 2010, Doherty et al. 2013). We stratified the PPR into 12 strata based on state and provincial boundaries and 3 prominent ecological regions in the study area adapted from the North American Level III Ecoregions to aid in the interpretation of our results (Wiken et al. 2011; Fig. 1). These strata allowed for consistent interpretation along prominent political and ecological boundaries in the PPR. Although similar in location and size, our strata should not be confused with the surveying strata used for collection and commonly used for analyses of the WBPHS data (e.g., Johnson and Grier 1988; see fig. 1 in Doherty et al. 2015).

METHODS

Data Sources

We used mallard count data recorded during the WBPHS conducted by the USFWS and CWS (Smith 1995). The survey was timed to coincide with peak mallard breeding abundance throughout their breeding range and generally conducted during 1–25 May in the PPR (Smith 1995). The survey was geographically stratified and conducted along static transects. Two observers fly transects 30–50 m above ground in fixed-wing aircraft to count all ducks observed within 200 m of each side of the transect. Transect lengths varied throughout the PPR according to strata boundaries and breeding duck densities. Counts were recorded sequentially along each transect on 28.8-km-long segments.

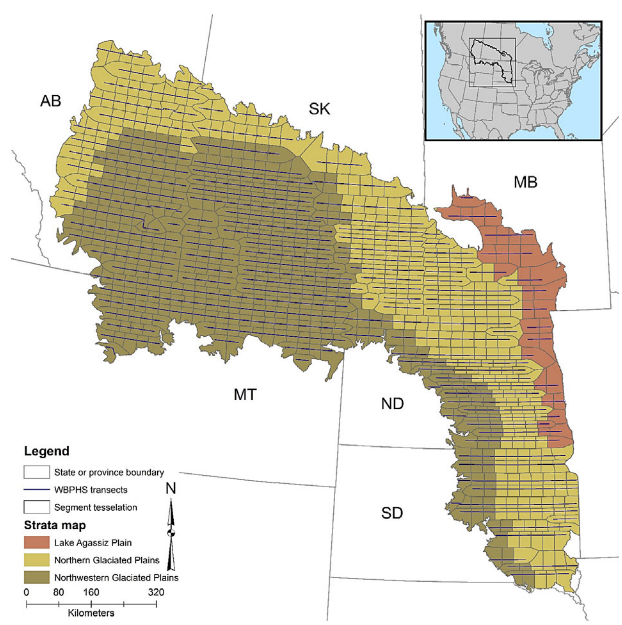

Figure 1. The Prairie Pothole Region (PPR) and associated ecological and state or provincial boundaries in the United States and Canada used to stratify interpretation of segment-level mallard counts recorded over 50 years of the Waterfowl Breeding Population and Habitat Survey (WBPHS) during 1964–2013. The segment tessellation was a grid created from a Euclidian allocation of PPR area to the nearest survey segment of the WBPHS.

We used segment-level counts in our analysis because they provided the finest-resolution measurement of mallard distribution in the study area. Segment-level data from the WBPHS have been used in other investigations to characterize local variability in pond or waterfowl counts (e.g., Podruzny et al. 2002, Howerter et al. 2014, Doherty et al. 2015) and provide an empirical description of within-year spatial heterogeneity in mallard distribution in the survey area.

The WBPHS began in 1955 and data were available from the first year onward. However, we constrained our analysis to the 50-year period between 1964 and 2013 because most of the PPR was surveyed annually during this period and ground crews calculated visibility correction factors (VCFs) for surveys conducted over the entire survey area during this period (Smith 1995). Mallards were enumerated in 3 categories during surveys: single males, pairs, and groups. We assumed a single unpaired male indicated a breeding pair and calculated total mallard counts for each segment as 2 times the number of single males and pairs plus the number of individuals in groups (Stewart and Kantrud 1972). We corrected raw counts with VCFs determined from ground surveys to account for visibility bias and variation among observers. We included all segments that were completely within the PPR in the analysis ($n = 769$; Fig. 1).

We created a tessellation grid around segments in the study area based on Euclidian allocation of area around each segment (Fig. 1). The procedure assigned all the land within the study area to the nearest survey segment, creating a gridded lattice of cells that correspond with the nearest survey segment. We used this grid to calculate a binary adjacency matrix for surveyed segments in each year (which accommodated variation in survey effort among years) that was used in the global and local statistics calculations and for visual interpretation of the results within our study strata and across the entire study area.

Statistical Analyses

We calculated the percentage of segments each year that comprised 90% of all the mallards counted in that year as an initial description of spatial heterogeneity in mallard distribution within the study region each year. We sorted segments surveyed in each year from greatest to fewest counts and calculated the proportion of segments it took to reach 90% of all the mallards counted. This qualitative metric allowed us to ask whether mallards were distributed roughly uniformly throughout the region (in which case the percent of segments comprising 90% of the mallards would be near 90%) or whether mallards were unevenly distributed (in which case 90% of mallards would be on <90% of the study area). The proportion of segments comprising 90% of mallards counted annually could potentially overestimate the total area within the study area on which 90% of the mallards occurred because survey transects were placed at slightly greater densities in areas with expected greater waterfowl abundances (Smith 1995). To test for such a bias, we ran a separate analysis that considered the total area of the tessellation grid around each segment that contributed to the first 90% of mallards counted in the survey area. We tested for differences between the percent of segments comprising 90% of mallards and percent of total area in the PPR comprising 90% of mallards with a paired t-test and found no differences in the 2 percentages ($t_{49} = 0.77$, $P = 0.44$). Therefore, we reported results of the analysis of total segments comprising 90% of the mallards counted within the PPR annually.

We calculated a general G-statistic in the *spdep* package in Program R as a quantitative test for global spatial autocorrelation in mallard abundance in each year (Getis and Ord 1992, Bivand 2014). The null hypothesis of the global spatial autocorrelation test was random distribution of mallard counts across the study area (Getis and Ord 1992). Although these results are informative in preliminary evaluation, the null hypothesis of no global spatial autocorrelation across the PPR is arguably naive because of the characteristic variability in land cover and climate across the region (Getis and Ord 1996). Local indicators of spatial autocorrelation (LISA) are more informative tests of the nature of autocorrelation across large spatial scales, because they allow investigators to ask where within the study area significant clusters of heterogeneous observations occurred and characterize the nature of those clusters through time (Anselin 1995, Getis and Ord 1996). We used the G_i^* test (Getis and Ord 1992), which is a LISA that compares local averages (mean values at point i and all neighbors within a specified distance) to global averages to find high-value ("hot spots") or low-value clusters ("cold spots"). The procedure is colloquially known as hot-spot analysis. We calculated G_i^* statistics for each year with the *spdep* package in Program R (Bivand 2014). The G_i^* test calculates a z-statistic for each segment based on a neighborhood adjacency matrix. The z-statistic and associated distribution can be used to indicate regions with statistically significant clusters of high (hot spots) or low values (cool spots). We used $\alpha = 0.05$ to assess significance of global spatial autocorrelation and as the threshold z-value to identify clusters (cold spots <-1.96, hot spots >1.96). We did not use a multiple comparisons correction because our analysis was exploratory and focused on inter-annual comparisons, rather than describing occurrence or characteristics of individual clusters (Caldas de Castro and Singer 2006).

We calculated an index (hereafter, hot-spot index) to facilitate comparison of the G_i^* results among strata and time periods. The hot-spot index was calculated as,

$$\text{Hot spot index} = \left(\frac{n_{hot}}{n_{total}} - \frac{n_{cold}}{n_{total}}\right) \times 100$$

where n_{total} was the total number of observations (either years or segments), n_{hot} was the number of observations that were classified as hot, and n_{cold} was the number of observations classified as cold. High values of the hot-spot index indicated the strata or segment had a high prevalence of significantly large count clusters, whereas negative values indicated an abundance of low counts. We plotted mean hot-spot index scores for each stratum in each year to qualitatively investigate spatial patterns in abundance through time. We also mapped mean segment-specific hot-spot indices for the entire study period and during 5 10-year periods to characterize the spatial distribution of hot-spot indices through time. We characterized variability in z-scores among years for each segment by calculating and mapping a coefficient of variation (CV) of scores over the study period. z-score statistics ranged from -3.7 to 9.1, so we added a constant (5) to each z-score to facilitate calculating the CV without zeroes or small positive numbers in the denominator. We calculated Pearson's correlation coefficients between z-scores and year for each segment to test for trends in z-scores through time and mapped significant ($P < 0.05$) trends over the study period to examine spatial patterns in declining or increasing z-scores.

RESULTS

We included an average of 754 segments/year in the analysis over the 50-year study period (range = 567–769 segments). Fewer segments were surveyed early in the study, when transects in the U.S. portion of the PPR (especially MT) were not operational. The proportion of segments comprising 90% of the total mallards counted within the study area ranged from 9.2% to 25.2% and averaged 15.3% of segments (SD = 3.7). The general G-statistic revealed strong evidence for global spatial autocorrelation in each year (all 50 annual $P < 0.001$).

The G_i^* analysis identified regions with clusters of high or low values in each year (Fig. S1, available online in Supporting Information). Mean counts in sequential 10-year periods in the analysis and annual plots of mean hot-spot index scores among strata revealed a general trend of increasing scores in the eastern portions of the study region in the Dakotas and central Saskatchewan and decreasing scores in northern and western portions in Alberta (Figs. 2–4). Montana and the Lake Agassiz Plain strata were consistently classified as cold spots and had below-average counts (Figs. 2–4). Western portions of the Canadian PPR and Dakota portion of the U.S. PPR showed the greatest variability in z-scores through time as indexed by CVs (Fig. 5). Most segments (73.6%) had significant correlations between z-scores and year. Inspection of the correlations by segment revealed a tendency for decreasing trends in the western portions of the study area and increasing or static trends in eastern portions of the study area (Fig. 6).

DISCUSSION

Considerable work has been conducted to address the socioeconomic and ecological complexity in the management of mallard populations and their habitats in the PPR (Johnson et al. 1997, 2002; Rashford et al. 2011; Doherty

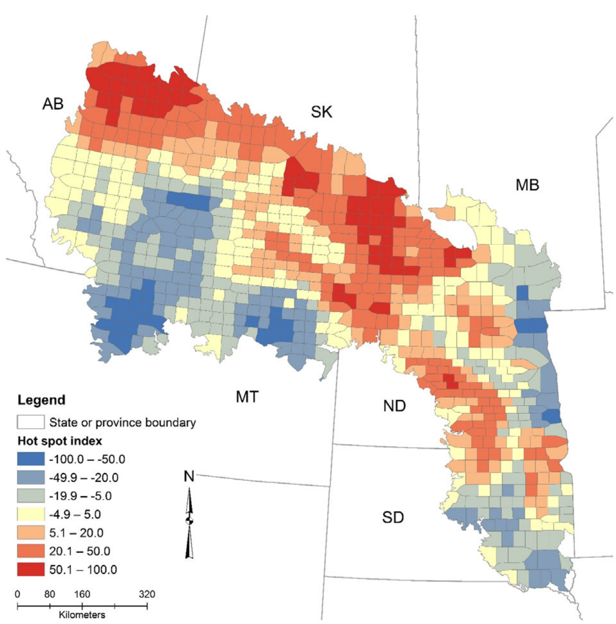

Figure 2. Mean hot-spot index scores based on mallard counts recorded on segments surveyed by the Waterfowl Breeding Population and Habitat Survey in the Prairie Pothole Region of the United States and Canada during 1964–2013. High values of the index (red regions) indicate frequent classification of the segment as high-count clusters (hot spots), whereas low values of the index (blue regions) indicate frequent classification as low-count clusters (cold spots).

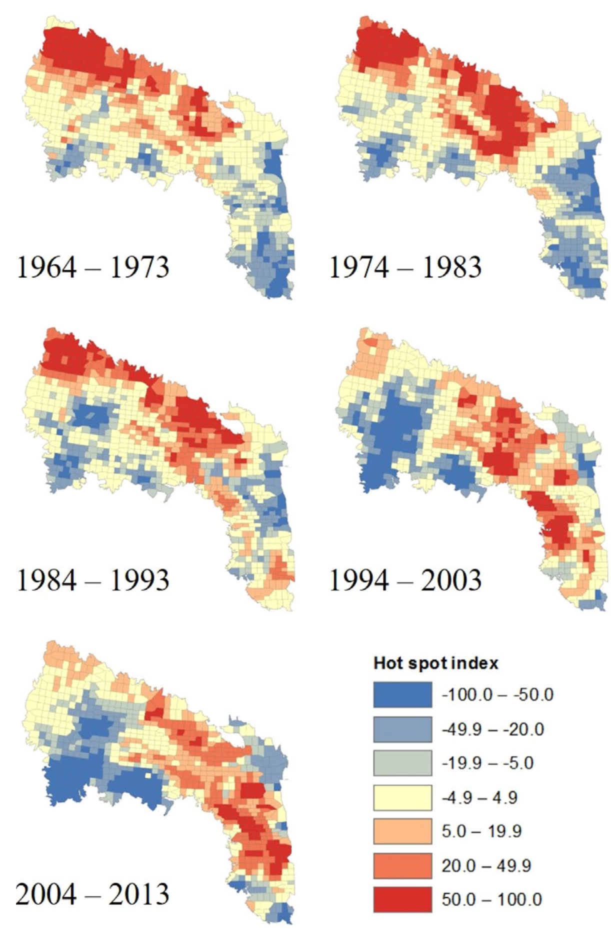

Figure 3. Mean hot-spot index scores over 10-year periods based on mallard counts recorded on segments surveyed by the Waterfowl Breeding Population and Habitat Survey in the Prairie Pothole Region of the United States and Canada during 1964–2013. High values of the index (red regions) indicate frequent classification of the segment as high-count clusters (hot spots), whereas low values of the index (blue regions) indicate frequent classification as low count clusters (cold spots).

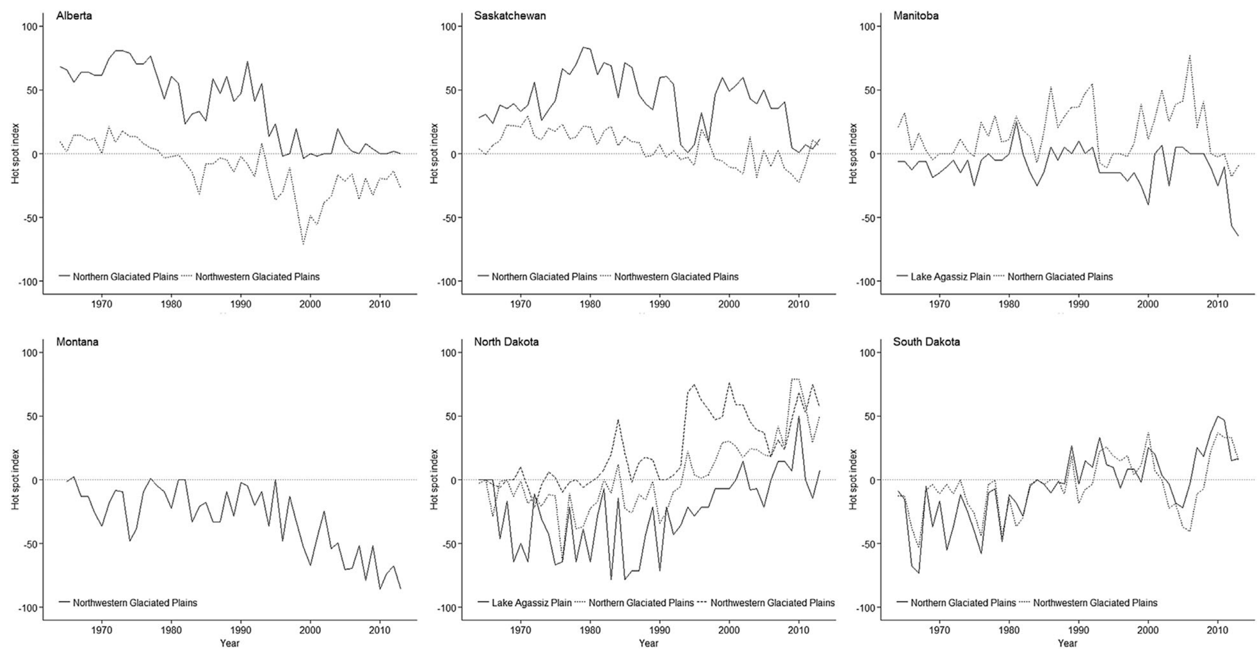

Figure 4. Mean annual hot-spot index scores within geopolitical strata in the Prairie Pothole Region of the United States and Canada based on mallard counts recorded on segments surveyed by the Waterfowl Breeding Population and Habitat Survey during 1964–2013. High values of the index indicate more segments were classified as high-count clusters (hot spots) in the strata, whereas low values of the index indicate more segments were classified as low-count clusters (cold spots).

et al. 2013, 2015; Walker et al. 2013*a*). Our study illustrated that although the PPR hosts a majority of breeding mallards counted in North America annually (Batt et al. 1989; Table S1), mallard distribution in the region was highly clustered and demonstrated substantial spatial heterogeneity throughout the late 20th century and early 21st century. This conclusion was first supported by the analysis of proportion of segments comprising 90% of mallards counted annually, which revealed mallard distribution within the PPR was

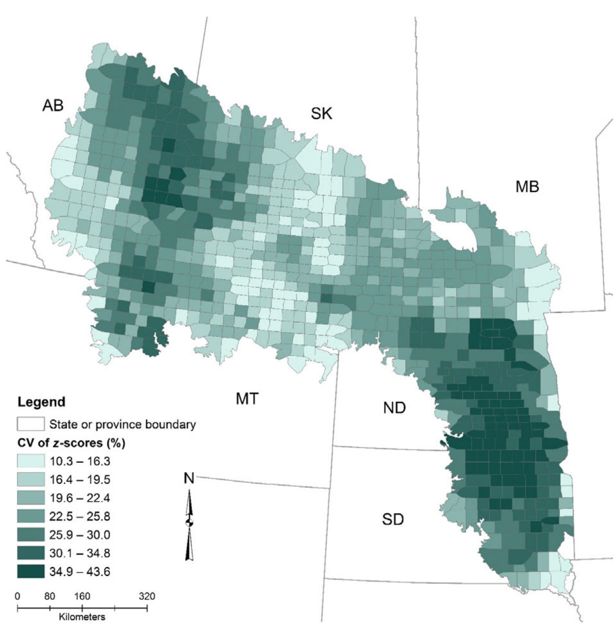

Figure 5. Map of segment-level coefficient of variability (CV) in z-scores calculated with a Getis G_i^* analysis of mallard counts recorded in the Prairie Pothole Region of the United States and Canada in association with the Waterfowl Breeding Population and Habitat Survey during 1964–2013. Higher CV values indicate increased heterogeneity of z-scores on the segment throughout the study period.

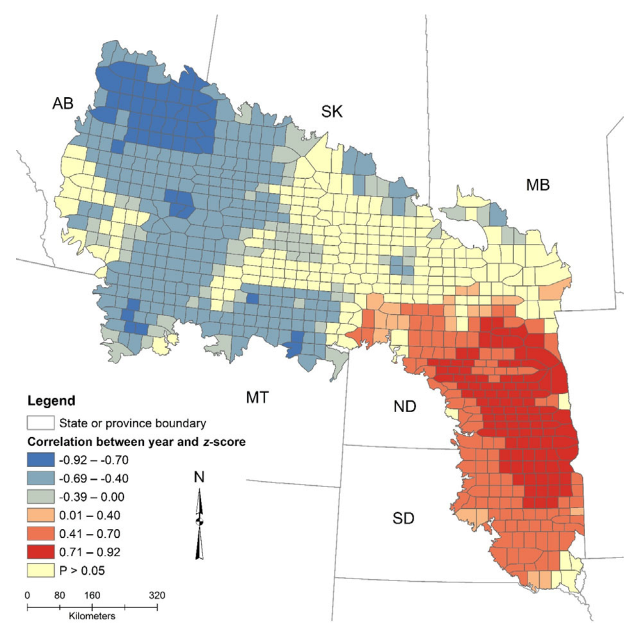

Figure 6. Map of Pearson's correlation coefficient between z-scores calculated with a Getis G_i^* analysis of mallard counts recorded in the Prairie Pothole Region of the United States and Canada in association with the Waterfowl Breeding Population and Habitat Survey during 1964–2013 and year of the score. Insignificant correlations ($P > 0.05$) are indicated in tan, whereas positive correlations (increasing through time) are indicated in red, and negative correlations (decreasing through time) are indicated in blue.

annually constrained to an average of only 15%, and never exceeded 25%, of surveyed segments. Converting these percentages to areas reveals 127,500–212,500 km^2 in the PPR annually hosted a decisive majority of all the mallards settling in the region. Accordingly, if conservation strategies aim to improve or conserve habitats in the core breeding range of mallards, such efforts should benefit from identifying regions consistently included or omitted from this small proportion of the region. Our hot-spot analysis was a first step in this vein, revealing a dynamic distribution of hot spots through time, which suggests although mallards consistently clustered on approximately 15% of the area, the location of these small breeding cores were a moving target across the northern and eastern parts of PPR.

Many factors likely contributed to the observed spatial heterogeneity of mallard abundance in the PPR during our study period. Our objective was to test for and describe heterogeneity in distribution through time, rather than to evaluate mechanisms responsible for observed distribution patterns. However, a review of the literature on mallard breeding ecology in the PPR revealed a number of factors that could have contributed to or interacted to produce the spatial patterns we observed; understanding these factors is important to prioritizing conservation efforts in the region. The first apparent spatial pattern observed during this study was the tendency for certain areas within the PPR to be consistently classified as cold spots, namely the Montana portion of the PPR, southwestern Saskatchewan, southeastern Alberta, and the Lake Agassiz Plain in eastern North Dakota and Manitoba. Eastern areas with low annual abundances, namely the Lake Agassiz Plain, were likely so because of the low availability of nesting cover and wetland habitats within the relatively flat, intensively modified terrain (Austin et al. 2001, Doherty et al. 2013). Western areas with low annual abundance were in regions with less annual precipitation and noted for their comparatively arid and periodic precipitation regimes that influence wetland availability (Ball et al. 1995, Millett et al. 2009). Such arid regions, although important for other species of breeding waterfowl tolerant of drier conditions such as northern pintail (*Anas acuta*) and American wigeon (*A. americana*; Johnson and Grier 1988), likely make comparatively few contributions to annual mallard production in the PPR.

Beyond the few regions with low annual abundances of mallards, the remainder of the PPR hosted high densities of mallards at some point over the 50-year study period. There was, however, substantial temporal autocorrelation in the location of hot spots through time, leading to an apparent shift of core breeding populations from the northwestern PPR into the Dakotas over the study period. Many studies have identified habitat factors that drive breeding mallard abundance through time at experimental scales ranging from individuals (e.g., Krapu et al. 1997, Howerter et al. 2014) to the entire North American breeding range (e.g., Johnson and Grier 1988). Miller (2000) examined factors affecting mallard distribution in the PPR and reported mallards in the eastern PPR generally responded to variation in wetland conditions, whereas mallards in the northwestern portions of the PPR responded to variation in upland habitat. Miller's (2000) analysis aids interpretation of our results because it illustrated that single causative factors were unlikely to drive spatial heterogeneity of hot spots. Rather, interactions between hydrologic conditions related to climate variation and variation in upland nesting habitat associated with agricultural land use likely drove observed patterns. Such systemic changes in habitat availability or quality, coupled with the tendency for mallards to demonstrate strong breeding-site fidelity, can lead to positive feedbacks, where increasing densities in response to favorable habitat conditions in one year begets increased densities in subsequent years ultimately leading to systematic shifts in densities observed through time (Dufour and Clark 2002).

Wetland conditions, driven primarily by climatic variation, are an important determinant of the spatial distribution of mallards within the PPR, as evidenced by the well-documented and widely cited positive association between waterfowl abundance and annual indices of wetland abundance collected in association with the WBPHS (i.e., pond counts; Johnson and Shaffer 1987, Kaminski and Gluesing 1987, Johnson and Grier 1988, Bethke and Nudds 1995, Doherty et al. 2015). Drever (2006) found wetland conditions indexed by pond counts lead to spatial synchrony in mallard abundance within the PPR, providing a mechanism for observed spatial clustering reported in this study. Trends in pond counts in the U.S. PPR appear to qualitatively correlate with observed shifts in distribution of hot spots through time reported in this study: drier periods in the 1970s through early 1980s were associated with periods of low abundance and few hot-spots in the Dakotas, while increases in abundance and hot-spots through the late 20th century and early 21st century corresponded with increases in wetland abundance in the region (see fig. 1 in USFWS [2013] for pond trends). A significant trend in pond abundance in prairie Canada was less apparent (fig. 1 in USFWS [2013]), but a redistribution of pond counts (perhaps from west to east) within the region could go undetected in the coarse spatial scale reported for the Canadian prairies.

Recent research has illustrated the importance of wetland dynamics associated with wet–dry cycles of prairie wetlands in reproductive success of mallards (Walker et al. 2013*b*), suggesting wetland dynamics may also serve as a settling cue for prebreeding mallards and therefore, underlie observed spatial heterogeneity in hot spots detected in our study. Interestingly, simulation models of prairie wetland hydrology presented by Werner et al. (2013) suggested a decline in wetland hydrologic cycling related to climate change had occurred in the northwestern portions of the PPR in the late 20th century, roughly coincident with the declines we observed in mallard hot spots in the region. This coincidence may suggest chronic climatic shifts associated with anthropogenic climate change may have already manifested in the PPR during a period of relatively favorable hydrologic conditions. This finding underscores the potential vulnerability of mallards to climate change during drier periods or spatial shifts in climatic conditions that produce favorable wetland conditions for mallards and merits additional consideration among researchers and conservation planners (Sorenson et al. 1998, Johnson et al. 2010).

Changes in land use throughout the region and its interactions with climatic conditions also likely contributed to observed spatial patterns of mallard hot spots (Bethke and Nudds 1995). Land-use changes have direct implications in their capacity to reduce upland nesting potential (e.g., Higgins 1977, Cowardin et al. 1985) and less obvious but potentially important effects on wetland hydrology in response to upland land uses (e.g., Euliss and Mushet 1996, Voldseth et al. 2007, McCauley et al. 2015). Shifts in mallard abundance related to land-use change may have been pervasive in the northwestern PPR where the greatest decline in mallard hot spots occurred. Previous research in that region documented effects of changing agricultural land uses on waterfowl (Bethke and Nudds 1995, Miller 2000, Podruzny et al. 2002). Specifically, expansion of agriculture onto marginal lands, abandonment of cropping practices that create favorable nesting cover (e.g., summer fallow, planting of winter wheat), and conversion of pastures to cropland were ubiquitous across the region during the latter years of the study (Bethke and Nudds 1995, Podruzny et al. 2002, Rashford et al. 2011). In a rough contrast, increases in mallard hot spots in U.S. portions of the PPR appeared to coincide with increases in suitable nesting cover in the region associated with implementation of the Conservation Reserve Program (CRP) following passage of the Food Security Act of 1985 (Reynolds et al. 2001, 2006). This, combined with the aforementioned improvements in climatic conditions for wetlands, may have facilitated the increased hot spots in U.S. PPR during the study. However, the region still experienced substantial land-use changes during the late 20th and early 21st centuries associated with ongoing wetland drainage (Oslund et al. 2010, McCauley et al. 2015), changes in cropping practices from mostly small grains to corn and soybeans (Higgins et al. 2002, Johnston 2014), and conversion of native grasslands or land formerly enrolled in the CRP to cropland (Stephens et al. 2008, Doherty et al. 2013, Wright and Wimberly 2013). That these wide-spread land-use changes coincided with increases in mallard hot spots in the region suggests wetland conditions as driven by climatic variability may be the primary driver of mallard abundance in the Dakotas (Krapu et al. 1983, Miller 2000). Further, perhaps the full potential of the region under the favorable climatic conditions in the latter half of the study period was not realized because of the limitations imposed by ongoing upland and wetland habitat loss.

MANAGEMENT IMPLICATIONS

Our results, when considered in concert with other key decision metrics such as land valuation (Rashford et al. 2011), demographic performance (e.g., Howerter et al. 2014), and land conversion risks (e.g., Stephens et al. 2008), should help inform conservation efforts within the PPR by helping to identify areas to deemphasize or prioritize. Our retrospective approach suggests prevailing environmental and land-use conditions in the western PPR precluded widespread use by mallards and, thus, this area may merit less emphasis for mallard-focused conservation efforts. Our results similarly offer promise for identifying and prioritizing efforts to affect the 15% of the area in which mallards settled in highest densities. However, translating this annually small geographic footprint into effective conservation will be constrained by the dynamic distribution of the core breeding population we documented. To confront this challenge, researchers should seek to understand the mechanisms driving these shifts and evaluate the potential for control over important drivers in the region. Our finding of an apparent shift of core-portions of the mallard population into the Dakotas during the wet period of the late 20th and early 21st century may illustrate the resiliency of mallard populations to ongoing land-use change in the region when constraints on wetland habitat were satisfied. This argument is bolstered by the population growth of mallards, which has been shown in the WBPHS and independent band-recovery analyses (Alisauskas et al. 2014), that coincided with the spatial redistribution of the core breeding areas during the recent wet period on the U.S. PPR. These observations arguably suggest climate-driven wetland dynamics may be more influential than land-use change, which has substantial implications for wetland restoration strategies in the region. Finally, the dynamic distribution of core breeding populations we documented suggests spatial redundancy in conservation allocation is likely necessary to accommodate naturally dynamic climatic suitability in the region.

ACKNOWLEDGMENTS

We acknowledge and thank the survey crews and administrative staff that worked with the U.S. Fish and Wildlife Service and Canadian Wildlife Service for their extensive efforts in coordinating and collecting the survey data used in the present analyses. J. Walker, K. Doherty, T. Arnold, D. Howerter, and J. Leafloor each provided constructive comments on earlier drafts that considerably improved the quality and presentation of the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

Alisauskas, R. T., T. W. Arnold, J. O. Leafloor, D. L. Otis, and J. S. Sedinger. 2014. Lincoln estimates of mallard (*Anas platyrhynchos*) abundance in North America. Ecology and Evolution 4:132–143.

Anselin, L. 1995. Local indicators of spatial association—LISA. Geographical Analysis 27:93–115.

Austin, J. E., T. K. Buhl, G. R. Guntenspergen, W. Norling, and H. T. Sklebar. 2001. Duck populations as indicators of landscape condition in the Prairie Pothole Region. Environmental Monitoring and Assessment 69:29–47.

Ball, I. J., R. L. Eng, and S. K. Ball. 1995. Population density and productivity of ducks on large grassland tracts in northcentral Montana. Wildlife Society Bulletin 23:767–773.

Batt, B. D. J., M. G. Anderson, C. D. Anderson, and F. D. Caswell. 1989. The use of prairie potholes by North American ducks. Pages 204–227 *in* A. G. Van der Valk, editor. Northern prairie wetlands. Iowa State University Press, Ames, USA.

Bethke, R. W., and T. D. Nudds. 1995. Effects of climate-change and land-use on duck abundance in the Canadian prairie-parklands. Ecological Applications 5:588–600.

Bivand R. 2014. spdep: spatial dependence: weighting schemes, statistics and models. R package version 0.5-74. http://CRAN.R-project.org/package=spdep.

Bradbury, R. B., R. J. H. Payne, J. D. Wilson, and J. R. Krebs. 2001. Predicting population responses to resource management. Trends in Ecology & Evolution 16:440–445.

Caldas de Castro, M., and B. H. Singer. 2006. Controlling the false discovery rate: a new application to account for multiple and dependent tests in local statistics of spatial association. Geographical Analysis 38:180–208.

Cowardin, L. M., D. S. Gilmer, and C. W. Shaiffer. 1985. Mallard recruitment in the agricultural environment of North Dakota. Wildlife Monographs 92.

Cowardin, L. M., T. L. Shaffer, and P. M. Arnold. 1995. Evaluations of duck habitat and estimation of duck population sizes with a remote-sensing based system. National Biological Service, Biological Science Report 2. Jamestown, North Dakota, USA. Northern Prairie Wildlife Research Center Online. http://www.npwrc.usgs.gov/resource/birds/duckhab/index.htm (Version 16JUL97).

Devries, J. H., R. W. Brook, D. W. Howerter, and M. G. Anderson. 2008. Effects of spring body condition and age on reproduction in mallards (*Anas platyrhynchos*). Auk 125:618–628.

Doherty, K. E., J. S. Evans, J. Walker, J. H. Devries, and D. W. Howerter. 2015. Building the foundation for international conservation planning for breeding ducks across the U.S. and Canadian border. PLoS ONE 10: e0116735.

Doherty, K. E., A. J. Ryba, C. L. Stemler, N. D. Niemuth, and W. A. Meeks. 2013. Conservation planning in an era of change: state of the U.S. Prairie Pothole Region. Wildlife Society Bulletin 37:546–563.

Drever, M. 2006. Spatial synchrony of prairie ducks: roles of wetland abundance, distance, and agricultural cover. Oecologia 147:725–733.

Dufour, K. W., and R. G. Clark. 2002. Differential survival of yearling and adult female mallards and its relation to breeding habitat conditions. Condor 104:297–308.

Euliss, N. H., and D. M. Mushet. 1996. Water-level fluctuation in wetlands as a function of landscape condition in the prairie pothole region. Wetlands 16:587–593.

Franklin, J. 2010. Moving beyond static species distribution models in support of conservation biogeography. Diversity and Distributions 16:321–330.

Getis, A., and J. K. Ord. 1992. The analysis of spatial association by use of distance statistics. Geographical Analysis 24:189–206.

Getis, A., and J. K. Ord. 1996. Local spatial statistics: an overview. Pages 261–277 *in* P. Longley, and M. Batty, editors. Spatial analysis: modelling in a GIS environment. John Wiley and Sons, New York, New York, USA.

Higgins, K. F. 1977. Duck nesting in intensively farmed areas of North Dakota. Journal of Wildlife Management 41:232–242.

Higgins, K. F., D. E. Naugle, and K. J. Forman. 2002. A case study of changing land use practices in the Northern Great Plains, USA: an uncertain future for waterbird conservation. Waterbirds 25:42–50.

Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, and I. J. Ball. 2002. Sensitivity analyses of the life cycle of midcontinent mallards. Journal of Wildlife Management 66:883–900.

Howerter, D. W., M. G. Anderson, J. H. Devries, B. L. Joynt, L. M. Armstrong, R. B. Emery, and T. W. Arnold. 2014. Variation in mallard vital rates in Canadian Aspen Parklands: the Prairie Habitat Joint Venture assessment. Wildlife Monographs 188.

Johnson, D. H., and J. W. Grier. 1988. Determinants of breeding distributions of ducks. Wildlife Monographs 100.

Johnson, D. H., and T. L. Shaffer. 1987. Are mallards declining in North America? Wildlife Society Bulletin 15:340–345.

Johnson, F. A. 2011. Learning and adaptation in the management of waterfowl harvests. Journal of Environmental Management 92:1385–1394.

Johnson, F. A., W. L. Kendall, and J. A. Dubovsky. 2002. Conditions and limitations on learning in the adaptive management of mallard harvests. Wildlife Society Bulletin 30:176–185.

Johnson, F. A., C. T. Moore, W. L. Kendall, J. A. Dubovsky, D. F. Caithamer, J. R. Kelley, and B. K. Williams. 1997. Uncertainty and the management of mallard harvests. Journal of Wildlife Management 61:202–216.

Johnson, R. R., and K. E. Higgins. 1997. Wetland resources of eastern South Dakota. South Dakota State University, Brookings, USA.

Johnson, W. C., B. Werner, G. R. Guntenspergen, R. A. Voldseth, B. Millett, D. E. Naugle, M. Tulbure, R. W. H. Carroll, J. Tracy, and C. Olawsky. 2010. Prairie wetland complexes as landscape functional units in a changing climate. BioScience 60:128–140.

Johnston, C. A. 2014. Agricultural expansion: land use shell game in the U.S. Northern Plains. Landscape Ecology 29:81–95.

Kaminski, R. M., and E. A. Gluesing. 1987. Density-related and habitat-related recruitment in mallards. Journal of Wildlife Management 51:141–148.

Krapu, G. L., R. J. Greenwood, C. P. Dwyer, K. M. Kraft, and L. M. Cowardin. 1997. Wetland use, settling patterns, and recruitment in mallards. Journal of Wildlife Management 61:736–746.

Krapu, G. L., A. T. Klett, and D. G. Jorde. 1983. The effect of variable spring water conditions on mallard reproduction. Auk 100:689–698.

McCauley, L. A., M. J. Anteau, M. Post van der Burg, and M. T. Wiltermuth. 2015. Land use and wetland drainage affect water levels and dynamics of remaining wetlands. Ecosphere 6:92. http://dx.doi.org/10.1890/ES14-00494

Miller, M. W. 2000. Modeling annual mallard production in the prairie-parkland region. Journal of Wildlife Management 64:561–575.

Millett, B., W. C. Johnson, and G. Guntenspergen. 2009. Climate trends of the North American prairie pothole region 1906–2000. Climatic Change 93:243–267.

Munro, R. E., and C. F. Kimball. 1982. Population ecology of the mallard VII. Distribution and derivation of the harvest. U.S. Fish and Wildlife Service Resource Publication 147, Washington, D.C., USA. http://pubs.er.usgs.gov/publication/5230180.

Niemuth, N. D., B. Wangler, and R. E. Reynolds. 2010. Spatial and temporal variation in wet area of wetlands in the Prairie Pothole Region of North Dakota and South Dakota. Wetlands 30:1053–1064.

North American Waterfowl Management Plan [NAWMP] Committee. 2012. North American waterfowl management plan 2012: people conserving waterfowl and wetlands. Washington, D.C., U.S. Department of the Interior, Environment Canada, and Environment and Natural Resources Mexico. http://nawmprevision.org/.

Oslund, F. T., R. R. Johnson, and D. R. Hertel. 2010. Assessing wetland changes in the prairie pothole region of Minnesota from 1980 to 2007. Journal of Fish and Wildlife Management 1:131–135.

Podruzny, K. M., J. H. Devries, L. M. Armstrong, and J. J. Rotella. 2002. Long-term response of northern pintails to changes in wetlands and agriculture in the Canadian Prairie Pothole Region. Journal of Wildlife Management 66:993–1010.

Rashford, B. S., C. T. Bastian, and J. G. Cole. 2011. Agricultural land-use change in prairie Canada: implications for wetland and waterfowl habitat conservation. Canadian Journal of Agricultural Economics 59:185–205.

Reynolds, R. E., T. L. Shaffer, C. R. Loesch, and R. R. Cox. 2006. The farm bill and duck production in the Prairie Pothole Region: increasing the benefits. Wildlife Society Bulletin 34:963–974.

Reynolds, R. E., T. L. Shaffer, R. W. Renner, W. E. Newton, and B. D. J. Batt. 2001. Impact of the Conservation Reserve Program on duck recruitment in the US Prairie Pothole Region. Journal of Wildlife Management 65:765–780.

Smith, G. W. 1995. A critical review of the aerial and ground surveys of breeding waterfowl in North America. National Biological Service, Biological Science Report 5. U.S. Fish and Wildlife Service, Washington, D.C., USA.

Sorenson, L. G., R. Goldberg, T. L. Root, and M. G. Anderson. 1998. Potential effects of global warming on waterfowl populations breeding in the Northern Great Plains. Climatic Change 40:343–369.

Stephens, S. E., J. A. Walker, D. R. Blunck, A. Jayaraman, D. E. Naugle, J. K. Ringelman, and A. J. Smith. 2008. Predicting risk of habitat conversion in native temperate grasslands. Conservation Biology 22:1320–1330.

Stewart, R. E., and H. A. Kantrud. 1972. Population estimates of breeding birds in North Dakota. Auk 89:766–788.

U.S. Fish and Wildlife Service [USFWS]. 2013. Waterfowl population status, 2013. U.S. Department of the Interior, Washington, D.C. USA.

Voldseth, R. A., W. C. Johnson, T. Gilmanov, G. R. Guntenspergen, and B. V. Millett. 2007. Model estimation of land-use effects on water levels of northern prairie wetlands. Ecological Applications 17:527–540.

Vrtiska, M. P., J. H. Gammonley, L. W. Naylor, and A. H. Raedeke. 2013. Economic and conservation ramifications from the decline of waterfowl hunters. Wildlife Society Bulletin 37:380–388.

Walker, J., J. J. Rotella, C. R. Loesch, R. W. Renner, J. K. Ringelman, M. S. Lindberg, R. Dell, and K. E. Doherty. 2013*a*. An integrated strategy for grassland easement acquisition in the Prairie Pothole Region, USA. Journal of Fish and Wildlife Management 4:267–279.

Walker, J., J. J. Rotella, S. E. Stephens, M. S. Lindberg, J. K. Ringelman, C. Hunter, and A. J. Smith. 2013*b*. Time-lagged variation in pond density

and primary productivity affects duck nest survival in the Prairie Pothole Region. Ecological Applications 23:1061–1074.
Werner, B. A., W. C. Johnson, and G. R. Guntenspergen. 2013. Evidence for 20th century climate warming and wetland drying in the North American Prairie Pothole Region. Ecology and Evolution 3:3471–3482.
Whittaker, R. J., M. B. Araújo, P. Jepson, R. J. Ladle, J. E. M. Watson, and K. J. Willis. 2005. Conservation biogeography: assessment and prospect. Diversity and Distributions 11:3–23.
Wiken, E., F. Jimenez Nava, and G. Griffith. 2011. North American Terrestrial Ecoregions—level III. Commission for Environmental Cooperation, Montreal, Canada.
Wilson, K. A., M. F. McBride, M. Bode, and H. P. Possingham. 2006. Prioritizing global conservation efforts. Nature 440:337–340.
Wright, C. K., and M. C. Wimberly. 2013. Recent land use change in the western Corn Belt threatens grasslands and wetlands. Proceedings of the National Academy of Sciences 110:4134–4139.

Associate Editor: Leafloor.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Table S1. Annual estimates of total mallard breeding population size from 1964 to 2013 in the entire Traditional Survey Area (TSA) of the Waterfowl Breeding Population and Habitat Survey (WBPHS), annual estimate of population size of mallards in the Prairie Pothole Region (PPR) survey area defined by Batt et al. (1989), and proportion of all mallards in the TSA in the PPR.

Figure S1. Annual hot spot and cold spot maps from Getis-Ord G_i^* statistics calculated for mallard counts recorded from 1964 to 2013 during the Waterfowl Breeding Population and Habitat Surveys in the Prairie Pothole Region. Red areas indicate significant ($\alpha = 0.05$) clusters of high values (hot-spots), blue areas indicate significant clusters of low values (cold-spots), tan areas indicate neutral values that were surveyed in that year, and white areas indicate segments that were not surveyed and therefore excluded from the analysis in that year. (gif.)